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Pollen grains in the identification and classification of plants. VII. The Ranunculaceae

R. P. Wodehouse

(with plate 20 and one text-figure)

The pollen grains of the Ranunculaceae comprise several forms of widely different aspect. For the most part these are obviously related to each other, but they show that several divergent trends of development are well established. A correct understanding of these forms is of the utmost importance on account of the key position assigned to the Ranunculaceae among the dicotyledons.

The basic form, the form which characterizes the pollen grains of more than half of the species studied, is typified by the grains of *Ranunculus* (fig. 7). It is provided with a fairly thin, flexible, but not distensible exine. The relatively huge changes in volume to which pollen grains are always subjected with changing moisture content are accommodated by three long meridonally arranged furrows, called germinal furrows because they also permit the emergence of the pollen tube at time of germination. Each is crossed by a delicate elastic membrane which is nearly always flecked with fragments of material closely resembling that of the exine. When the grains are moist and fully expanded these flecks stand apart from each other, exposing much of the stretched membrane, but when the grains are even moderately dry and partly contracted the flecks are pressed closely together and against the margins of the furrow so that the grain is protected by what amounts to a continuous covering of exine throughout its entire surface. These furrows are further characterized by the total absence of germ pores—the whole furrow area serving as a place of emergence for the pollen tube—and by lack of thickened furrow rims, in these respects differing from perhaps the majority of three-furrowed grains of other families. The furrow margins are most commonly poorly defined, the texture of the general surface of the exine merging into the flecked surface of the furrow membrane, the two sometimes not even distinguishable from each other, unless the grains are expanded when the furrows are revealed by the separation of the flecks on their membranes as they stretch. The furrow margins are generally rough, jagged, or even fimbriate, sending long processes of exine-like material out onto the furrow membrane. These characters of the furrows, while undergoing some modifications within the family, are peculiar to the Ranunculaceae and, to a lesser extent, some of the more primitive monocotyledons, and are of profound phylogenetic significance.

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The mechanism whereby the furrows permit changes in volume without rupturing the exine is rather complex, but may be resolved into three more or less distinct movements. When a grain such as that of *Caltha*, for example, is quite dry and of its minimum volume, it is of an elongate form, perhaps twice as long as broad (fig. 10), and provided with three deep longitudinal grooves so that in section it appears deeply three lobed. With the expansion due to taking up moisture the first movement is the pushing out of the grooves until the grain becomes ellipsoidal and more nearly circular in outline, the furrows up to this stage remaining unexpanded and merely acting as hinges. In some grains in which the furrows are demobilized by heavy encrustations of exine material on their membranes the *hinge action* is the only movement permitted them, such grains remaining elongate even when fully expanded, for example those of *Adonis* (fig. 9). More often, however, as the turgidity of the grain increases the furrows expand, stretching their elastic membranes and becoming spindle shaped, the grain at the same time becoming shorter and broader until it is almost spherical or even oblately flattened, but still circular in section (fig. 4). This *furrow expansion* appears to be the most effective movement in the adjustment of volume, for, by changing its shape from ellipsoidal to spheroidal, the volume of the grain is greatly increased with a small amount of stretching of its furrow membranes and without materially increasing its surface. The majority of grains appear to require no further increase in volume than is permitted by the mechanism of furrow expansion. Further increase in volume, however, may be achieved by an outward distension of the furrow membranes forming a sort of aneurysm at each of the furrows, if I may be permitted to borrow a medical term which is used to describe the sudden distension of an artery wall to the limit if its elasticity under the influence of either excessive pressure from within the artery or a loss of tension of its wall. *Membrane distension* of this kind in pollen grains is generally accompanied by a flattening of the walls of the grain in the equatorial region, especially if the exine is thin, the grain assuming a rounded-triangular outline (fig. 1).

Among the tricolpate grains of the Ranunculaceae generally all three of these movements are more or less involved, but in the pollen of the majority of species furrow expansion is the favored movement, hinge action and membrane distension playing relatively minor rôles. Hence it is that the furrows of the grains described in the following pages are generally long and tapering to narrowed or pointed ends (fig. 7), for this kind of furrow is best adapted to the expansion movement. Those in which the hinge action is paramount are long and narrow, and not generally tapering much (fig. 9). And those in which membrane distension is

the major function are broad, generally rather short, and with broad rounded ends (fig. 2). It is in these furrow characters that differences between the different species are mainly expressed, especially among those which are closely related. Their phylogenetic significance is not deep seated, closely related species often showing rather extreme differences in these respects.

The characters of the exine show much less variation and appear to be phylogenetically much more deep seated than those of the mechanical action of the furrows. In its basic form the exine is rather thin—thin enough to be freely flexible, but thick enough to be indistensible—more or less granular and covered with minute papillae which are irregular in arrangement and various in size. In the grains of some species papillae are strongly developed, almost reaching the size of spines; in others they are vestigial or even entirely absent, this condition being generally associated with correspondingly more pronounced granulation of the exine. Occasionally the papillae appear to coalesce forming a rudimentary reticulum (*e.g. Nigella*). For the most part the different species exhibit only different degrees in the relative development of the granular and papillate characters, but there are two other types of exine found within the family which have no obvious connection with these. One is the striate, found only in the three species of *Trollius* and the other is the pitted or reticulate, found in the grains of *Helleborus*, *Hydrastis* and *Paeonia* (fig. 1). The striate form can, perhaps, be interpreted as a derivative of the ordinary granular form in which the granules are arranged in rows; and possibly the reticulate form can be regarded as representing the coalescence of the papillae already initiated in the grains of *Nigella*. This latter, however, is uncertain because the reticulum of all the truly reticulate grains is much finer than that adumbrated in the grains of *Nigella*.

The basic form of grain of the Ranunculaceae may, therefore, be described as: approximately spheroidal, tricolpate; furrows long, broad and tapering to narrowed ends, their membranes flecked, their margins rough, jagged, or fimbriate; exine rather thin, more or less granular and papillate; in size various from about 20–30μ in diameter. Such a form is illustrated by the grain of *Ranunculus* (fig. 7), and characterizes, without serious modification those of about 20 of the 29 genera examined in this study (see key, p. 500).

The most important modifications of this basic form have to do with the furrows. The flecks on the furrow membrane, copious but discrete and irregular in arrangement in the basic form, are reduced in number or entirely absent in the grains of *Paeonia* (fig. 1). In others they are aggregated in various ways forming irregular patches or strips of exine-like

material on the furrow membrane, often fused to the furrow margins forming fimbriae, as in the grains of *Eranthus*, or aggregated in a central strip, as in those of *Hepatica*. The culmination of this developmental tendency seems to be reached in the grains of *Adonis aestivalis* (fig. 9), in which the furrow membrane is heavily encrusted with a central strip of exine material, and the furrows partly demobilized, deprived of nearly all movement except their hinge action.

Another modification is the substitution of rounded or irregularly shaped pores for the furrows in such grains as those of *Coptis*, *Syndesmon* and *Thalictrum* (figs. 3, 5, 8). The pores of these grains have all the other more important characteristics of the furrows of their closest relatives, such as their flecked membranes and their rough, jagged or fimbriate margins. In their number and arrangement, however, they do not always conform to the trischistoclasic system which governs the arrangement of the furrows, and in their harmomegathic function they possess only that of membrane distention, compensating for the lack of hinge action and furrow expansion by their larger number.

The pored form appears to have originated in this family more than once independently and at widely different times. It occurs in the anemophilous genus *Thalictrum*. Whether or not in this case there is any relation between anemophily and the pored condition can not be said, though the occurrence in this genus of both conditions which are exceptional in the family, suggests that there may be. The pored condition occurs in the Malayan genus *Naravelia*. These are woody climbers distinguished by the possession of connate carpels, divergent in this and in their southward distribution from the central ranalean type. In these two cases, at least, the pored character belongs to divergent groups, suggesting that it may be of recent origin. The same character, however, occurs in the grains of *Coptis trifolia* and *Xanthorrhiza apiifolia*. Both are North American plants, the former a herb of northern latitudes, occurring as far north as British Columbia and Alaska, the latter a shrub of more southern latitudes, from southern New York to Kentucky and Florida. The plants have so many things in common—their yellow roots, their bitter taste, their shining leaves which are trifoliate when basal—besides the practical identity in form of their pollen grains, that there can be little doubt that they are closely related. Possibly *Coptis* may be regarded as a northern herbaceous off-shoot from some ancestral stock of which *Xanthorrhiza* is a conservative survivor of more temperate regions. It would, therefore seem that, in this case at least, the pored character of the pollen grain is more ancient than the herbaceous habit. The same character is found in the grains of *Anemone coronaria* but is absent from the five other species

of *Anemone* which I have examined. These four rather widely separated occurrences suggest that this character has originated among the Ranunculaceae more than once. It is perhaps to be regarded as only a tendency in this family, and we may expect to find it more fully expressed in some of the derivatives of the Ranalean complex.

The ways in which pores have been derived from furrows is not entirely clear because most of the intermediate forms are lacking. Nevertheless, some of both the pored and furrowed grains of this family possess peculiar characteristics which are suggestive of how this might have come about. Among the pored grains the arrangement of the pores occasionally tends to conform to the trischistoclasic system as if the pores represented shortened furrows. In the grains of *Coptis* (fig. 3) and of *Xanthorrhiza*, for example, the pores are commonly arranged in triangular groups of three which suggest the triconvergent grouping of furrows arranged in this system. And in the grains of *Thalictrum dioicum* (fig. 8) the prevailing number of pores on the whole grain is six arranged exactly tetrahedrally, corresponding to the hexacolpate configuration of furrows. Such regularity of arrangement, however, is not the general rule. More typical is the condition found in the grains of *Syndesmon* (fig. 5). In these the pores are irregular in their size, shape and arrangement, they never suggest any complete furrow configuration, and frequently some are elongate, sometimes almost long enough to be regarded as furrows. Generally such elongate pores are curved or 'v' shaped and suggest that they may represent fragments of zonate and zigzag furrows. This is significant because among those grains of the family which have supernumerary furrows the ordinary furrow configurations are not usually found completely developed. The pollen of *Batrachium* is such an example. Here the grains all possess supernumerary furrows but instead of the usual symmetrical arrangements, the zonate, half zonate and zigzag arrangements are the most frequent. This is likewise true of the grains of *Ranunculus acris*. The furrows of these are also short and broadly rounded so that in many cases they have a striking resemblance to the elongate pores of the grains of *Syndesmon*. It would therefore seem that sometimes, as in the grains of *Coptis* and *Thalictrum*, the pores represent shortened furrows arranged in the trischistoclasic system, but in others, as in the grains of *Syndesmon* and *Anemone*, the pores represent fragments of furrows.

PAEONIA ALBIFLORA Pallas. Peony (fig. 1). Grains various, a large proportion of them obviously abortive. Normal grains oblate and triangular in outline when fully expanded, about 34μ in diameter, tricolpate. Furrows long, broad, and tapering to rounded ends, their membranes smooth or faintly flecked, their margins jagged but sharply defined. Exine moder-

KEY TO THE SPECIES

A. Exine granular, papillate, or both (papillae tending to fuse to form a reticulum in *Nigella*).
1. Furrows elongate, generally three meridionally arranged, though some grains of most species (all in *Pulsatilla alpina* and *Batrachium sp.*) may have higher numbers arranged irregularly or in the trischistoclasic system, their membranes more or less flecked.
i. Exine distinctly papillate and more or less granular.
a) Furrow ends broad and rounded.
1) Furrow margins smooth, and furrows broad, scarcely tapering.....Caltha
Anemone demissa
2) Furrow margins rough or jagged, and furrows tapering.
Grains more than 25 μ in diameter.....Ranunculus
Grains small, about 19 μ in diameter.....Isopyrum
b) Furrow ends pointed.....Pulsatilla
Hepatica
Eranthis
c) Furrow ends irregular and margins jagged.....Actaea
Cimicifuga
Anemone Davidi
quinquifolia
virginiana
Clematis
Myosurus
Oxygraphis
Trautvetteria
Batrachium
Nigella
Glaucidium
ii. Exine granular, scarcely or not at all papillate. Furrow ends pointed or somewhat blunt.
a) Furrows broad and tapering to pointed ends. Exine not excessively thick.
Grains slightly umbonate, 21–29 μ in diameter.....Aconitum
Delphinium
Grains not umbonate.....Aquilegia
b) Furrows narrow, partially demobilized by a heavy encrustation on their membranes. Exine excessively thick. Grains 25–27.5 μ in diameter.
Grains conspicuously umbonate. Exine only granular.....Adonis aestivalis
Grains not umbonate. Exine granular and faintly papillate.....Adonis vernalis
2. Furrows, in the ordinary sense, absent, their function being served by a number of rounded or irregularly shaped pores.
i. Exine distinctly papillate.
a) Grains small 16–18.5 μ in diameter.
Pores about 10, various.....Coptis
Pores 15 or more, circular.....Xanthorrhiza
b) Grains larger, over 22 μ in diameter.
Pores uniformly circular.....Anemone coronaria
Pores circular to elongate.....Syndesmon
ii. Exine granular, occasionally slightly papillate.....Naravelia
Thalictrum
B. Exine reticulate-pitted or frankly reticulate, furrows generally three meridionally arranged.
1. Furrow margins smooth.....Helleborus
2. Furrow margins rough.
i. Furrow membranes copiously flecked.....Hydrastis
ii. Furrow membranes nearly or quite smooth.....Paeonia
C. Exine striate, furrows generally three, their membranes flecked.....Trollius

ately thick, reticulate pitted. Intine thin, slightly thickened in the region underlying the furrow.

In the reticulate character of their exine these grains resemble those of *Helleborus* and *Hydrastis* but are otherwise unique in the family.

A garden perennial, native of Siberia, China and Japan.

GLAUCIDIUM PALMATUM S. & Z. Grains uniform, spheroidal, about 25.5μ in diameter, tricolpate. Furrows long and tapering to blunt ends, not excessively broad when expanded, their membranes conspicuously flecked and their margins jagged to almost fimbriate. Exine thin, papillate granular.

These grains conform in all respects with the basic form of the family but are dissimilar to those of *Paeonia* with which genus *Glaucidium* is associated in the tribe Paeonieae according to Engler.

The genus comprises only this species, native of Japan.

HYDRASTIS CANADENSIS L. Yellow root, yellow puccoon, golden seal. Grains uniform, spheroidal, 21–25.5μ in diameter, tricolpate. Furrows long and tapering, their membranes conspicuously flecked, their margins rough. Exine finely reticulate.

These grains resemble those of *Helleborus* in most respects. In their reticulate character, which is unusual in this family, they also resemble those of *Paeonia* with which they are associated in the tribe Paeonieae.

A low herbaceous perennial arising from a bright yellow rootstock. Native of the eastern United States and Canada.

CALTHA L. Marsh marigold

Grains uniform oblate and somewhat triangular in outline when expanded, 25–35μ in diameter, tricolpate. Furrows long and broad, scarcely tapering to broad rounded ends, their membranes more or less thickly covered with flecks, their margins smooth. Exine moderately thick, granular, and densely coated with minute papillae similar to the granules of the furrow membranes.

These grains differ from the type of the family only in the less papillate surface of the exine and broader furrows with smoother margins.

The genus comprises about 15 species of low marsh or semiaquatic herbs with large undivided leaves, generally cordate or reniform, distributed throughout the temperate and arctic regions of both hemispheres.

CALTHA PALUSTRIS L. Marsh marigold (fig. 2). Grains about 25μ in diameter. Furrow margins nearly or quite smooth, their membranes lightly flecked.

Native of northeastern United States and Canada.

CALTHA RADICANS Forst. Grains similar to those of *C. palustris*, their

furrow membranes more conspicuously flecked, their margins smooth but almost obscured by the granules of the furrow membranes.

The plant is similar to the above but roots from the lower nodes and has smaller flowers.

TROLLIUS L. Globeflower

Grains spheroidal or somewhat ellipsoidal, circular or three-lobed in outline, 17–26μ in diameter, tricolpate, occasionally some with aberrant numbers of furrows. Furrows long and tapering to irregularly shaped or rounded ends, their membranes flecked with granules, their margins smooth, granular, or even fimbriate. Exine thick and striate with the striae arranged in patterns resembling thumb-prints.

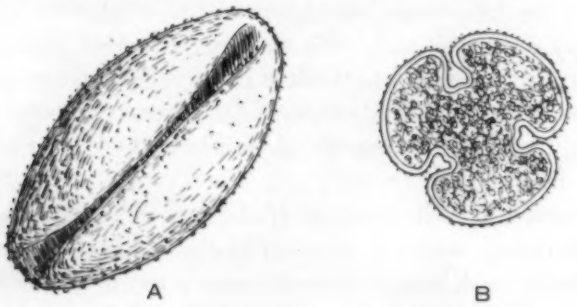

Fig. 10. *Caltha palustris*. A. Side view. B. transverse optical section.

The striate character of these grains has not been found elsewhere in this family, but similar markings are found on the grains of most Aceraceae and Rosaceae.

The genus comprises about 12 species of erect perennial ascending herbs resembling *Caltha*, mainly inhabiting marshy places. Native of the north temperate Zone.

TROLLIUS ALBIFLORUS (Gray) Rydbg. Grains uniform, spheroidal, about 25μ in diameter. Furrow margins fimbriate. Exine thick and rigid, thumb-print markings pronounced.

Herbaceous perennial of mountain tops, Colorado, and northward and westward.

TROLLIUS EUROPAEUS L. Globeflower. Grains ellipsoidal, three lobed in outline, tricolpate, 17–18$\times$20–22μ. Furrow margins rough but not quite fimbriate. Otherwise as in *T. albiflorus*.

Herbaceous perennial of wet uplands, northern Europe.

TROLLIUS LEDEBOURII Reichb. f. A large proportion of the grains small and apparently abortive. Normal grains 19–21μ in diameter,

spheroidal. Furrows long, broad and tapering to rounded ends, their margins smooth. Exine rather thick but less so than in *T. albiflorus* and the striate markings less conspicuous.

Herbaceous perennial occasionally found in cultivation, native of Siberia.

HELLEBORUS Tourn. Hellebore

Grains uniform excepting a few that are abortive, oblately flattened and triangular in outline when expanded, about 30μ in diameter, tricolpate. Furrows very broad and long, tapering to narrow but rounded ends, their membranes conspicuously flecked with rounded granules irregularly arranged, their margins smooth. Exine thin, finely and uniformly reticulate throughout, the reticulum ending with closed lacunae along the furrow margins.

These grains deviate rather widely from the type in the reticulate nature of their exine and the smooth margins of their furrows.

The genus comprises 15 perennial herbs with palmate leaves and large solitary nodding flowers appearing in early spring. Native of Europe and western Asia, some species introduced into North America, both wild and cultivated.

HELLEBORUS FOETIDUS L. Hellebore. Grains about 27.4μ in diameter. The ridges of the reticulum confluent along the margins of the furrows forming a thickened rim.

Native of northern Europe, cultivated elsewhere.

HELLEBORUS VIRIDIS L. Green hellebore. Grains as in *H. foetidus*

Native of Europe and Asia.

ERANTHIS LONGISTIPITATA Rgl. Winter aconite. Grains spheroidal or slightly oblately flattened, tricolpate. Furrows long, broad and tapering to narrowed but irregularly shaped ends, their membranes copiously flecked with large and coalescent granules, their margins jagged or fimbriate. Exine rather thick, papillate. Intine thick.

In these grains we see a most extreme manifestation of the tendency, characteristic of the family, for the furrow membranes to become obscured by granules of exine-like material. The granules resemble the papillae of the exine, they are large and coalescent with each other and with the jagged marginal projections forming fimbriae which reach almost entirely across the furrow.

The genus comprises about 7 species of perennial herbs with palmately multifid leaves from which arise one-flowered scapes surrounded by an involucre of a single leaf. Native of Europe, eastern and central Asia. *E. hyemalis* Salisb. sparingly naturalized in North America.

NIGELLA INTEGRIFOLIA Rgl. Fennel flower. Grains various, a large proportion abortive, normal grains oblately flattened, triangular in outline, 31–41μ in diameter, tricolpate. Furrows of medium length, broad and tapering to narrow but irregularly-shaped ends, their membranes flecked with granules similar to the papillae of the exine, their margins jagged and somewhat fragmenting. Exine thin, papillate with the papillae fusing to form an imperfect reticulum. Intine thick but not noticeably thicker in the regions of the furrows.

The papillae of the exine of these grains are similar to those of the furrow membranes, but in the latter situation they are more widely separated and appear to be sharply raised above the surface while on the exine they are less raised and more closely aggregated.

The genus comprises about 16 species, native of Europe.

ISOPYRUM L. Shell flower

Grains ellipsoidal to spheroidal, 18–19μ in diameter, tricolpate. Furrows long, broad and tapering, their membranes flecked, their margins rough. Exine rather thick, papillate.

Slender smooth perennial herbs with compound leaves and axillary white flowers resembling those of *Syndesmon*. The genus comprises about 30 species native of North America, Asia and Japan.

ISOPYRUM FUMARIOIDES L. Grains as in generic description, about19.4μ in diameter.

Native of Europe and northern Asia.

ISOPYRUM HENRYI Oliv. Grains as in the generic description, about 18.7μ in diameter.

Native of China.

COPTIS TRIFOLIA Salisb. Three-leaved goldthread (fig. 3). Grains spheroidal, 17–18.5μ in diameter. Pores about 10, their membranes flecked with conspicuous granules, generally prominently bulging, their margins fimbriate, various in size and shape but generally nearly circular. Exine rather thick, papillate.

These grains are similar to those of *Xanthorrhiza*, *Anemone coronaria Syndesmon*, *Naravelia* and *Thalictrum* within the family, but may be distinguished by the more fimbriate margins of their pores. Outside of the family they closely resemble the grains of the Alismaceae and some Butomaceae but may be distinguished from these by the character of their exine which is papillate while in these two latter families it is more nearly echinate.

The three-leaved goldthread is a low perennial herb with ternately divided root leaves, small white flowers on slender scapes, and roots of

long bright yellow fibers. Native of north eastern United States and Europe. The genus comprises about 8 species, principally of North America.

XANTHORRHIZA APIIFOLIA L'Her. (*X. simplicissima* Marsh.) Shrub yellowroot. Grains similar to those of *Coptis*, uniform. 16–18.5μ in diameter. Pores about 15, somewhat smaller than in the grains of *Coptis*, and their margins less conspicuously fimbriate.

A low shrubby plant with bark and roots deep yellow. Native of eastern United States from Pennsylvania southward.

A small genus of shrubby plants native of eastern North America cultivated for their foliage. The name is frequently written, *Zanthoriza*, an older form though etymologically incorrect.

ACTAEA SPICATA L. Baneberry. Grains uniform, oblate-spheroidal, 27–31μ in diameter, tricolpate. Furrows long, broad and tapering, their membranes conspicuously flecked, their margins ragged almost fimbriate. Exine rather thick, papillate.

A perennial herb in woods, northeastern United States and Canada. The genus comprises about 6 species native of the north temperate Zone.

CIMICIFUGA L. Black Cohosh, bugbane

Grains oblate spheroidal, 23–26μ in diameter, tricolpate. Furrows medium long, tapering to irregularly shaped ends; their membranes conspicuously flecked, their margins jagged, almost fimbriate. Exine thick and firm, granular, papillate and marked with angular areas enclosing the papillae. Intine thick and further thickened in the regions underlying the furrows.

The genus comprises eleven species of tall perennial herbs bearing long spikes of white flowers with the stamens exserted suggesting that they may be partly anemophilous, closely related to *Actaea*, widely distributed in the north temperate zone.

CIMICIFUGA DAHURICA Huth. Grains as in the generic description. Native of central Asia.

CIMICIFUGA FOETIDA L. Grains as in the generic description. Native of Europe and Asia.

AQUILEGIA L. Columbine

Grains spheroidal or slightly oblately flattened, rounded-triangular in outline, 21–29μ in diameter; tricolpate, generally some with supernumerary furrows. Furrows long, broad and tapering to pointed ends, their membranes conspicuously flecked, their margins differing in the different species from smooth to jagged or even somewhat fimbriate. Exine more or less

granular and minutely papillate, mostly thin but various in the different species. Intine thin and not visibly thickened in the regions of the furrows.

About 50 species of erect branching perennial herbs with compound leaves and large showy flowers, widely distributed throughout the north temperate zone.

AQUILEGIA CANADENSIS L. Wild columbine (type). Grains somewhat various; some obviously abortive, others with supernumerary furrows. Furrow membranes conspicuously flecked with granules irregularly arranged, furrow margins jagged or even somewhat fimbriate owing to the coalescence of some of the granules of the membrane with the jagged projection of the margins. Exine thin, faintly granular and finely papillate.

Perennial herbs in dry rocky woods almost throughout the eastern half of the United States and Canada.

AQUILEGIA VULGARIS L. Garden columbine. Grains mostly uniform, about 22μ in diameter, generally a small proportion tetra- and hexacolpate. Furrow membranes less conspicuously flecked than in the type.

Native of Europe and Siberia, widely cultivated in several varieties, and occasionally escaped in the United States.

AQUILEGIA GLANDULOSA Fisch. Grains uniform, about 21.6μ in diameter, tricolpate. Furrow membranes flecked with large and conspicuous granules, furrow margins rough. Exine thicker than in the type, slightly more granular, scarcely papillate.

Native of the Altai mountains, Siberia, but widely cultivated in the United States and elsewhere.

AQUILEGIA FLABELLATA S. & Z. Grains uniform, 25–29μ in diameter. Furrow membranes flecked with large conspicuous granules which tend to be arranged in rows, otherwise as in *A. glandulosa*.

Native of Japan but widely cultivated elsewhere.

DELPHINIUM L. Larkspur

Grains generally uniform, 25–29μ in diameter, spheroidal, ellipsoidal or slightly oblate, tricolpate, generally with a slight elongate mound due to the arching up of the exine, extending meridionally in each lune. Furrows, long, broad and tapering, their membranes conspicuously flecked with granules which tend to aggregate or coalesce into irregular groups, their margins roughened, jagged or fimbriate. Exine rather thin but somewhat thickened at the poles causing the grains to be slightly umbonate, finely but conspicuously granular.

These grains closely resemble those of *Aquilegia* but may be distinguished by their larger size, generally elongate and umbonate form.

The genus comprises about 250 species of perennial and annual erect herbs with showy flowers, in north temperate regions.

DELPHINIUM CAERLEUM Jacq. Grains spheroidal, ellipsoidal or slightly oblately flattened, about 28.5μ in diameter. Furrow margins roughened to fimbriate.

Native of Himalaya.

DELPHINIUM BULLEYANUM G. Forr. Grains spheroidal to ellipsoidal, about 27μ in diameter. Furrow margins jagged.

Native of China.

DELPHINIUM BONATII Léveillé. Grains ellipsoidal, about 25$\times$27μ. Furrow margins fimbriate.

Native of China.

ACONITUM L. Aconite, monkshood

Grains spheroidal, ellipsoidal, or more or less oblate, 21–27μ in diameter, tricolpate. Furrows long broad and tapering to irregularly shaped ends, their membranes copiously flecked with large granules, their margins jagged. Exine thin, finely granular.

These grains bear a close resemblance of those of *Delphinium* in the characters of their furrows and their exine, and two of the species here described are likewise umbonate.

Perennial herbs with palmately cleft or dissected leaves and showy flowers in racemes or panicles, closely resembling *Delphinium*. About 70 species in the higher parts of the north temperate zone.

ACONITUM DELPHINIFOLIUM DC. (fig. 4). Grains uniform, slightly oblately flattened, triangular in outline, 23–26μ in diameter, not umbonate.

Moist places, Alaska to Alberta to British Columbia.

ACONITUM DIVARICATUM Rydb. Grains spheroidal, scarcely three-lobed, 25–26μ in diameter. Otherwise as in *A. delphinifolium*.

Creek banks. Idaho to Utah to Wyoming.

ACONITUM HELLERI Greene. Grains spheroidal, ellipsoidal or slightly oblately flattened, 21.5–23μ in diameter, umbonate as in those of *Delphinium*.

Native of North America.

ACONITUM COLUMBIANUM Nutt. Western monkshood. Grains somewhat various, generally a large proportion abortive. Normal grains nearly spheroidal, 23–27.5μ in diameter, similar to those of *A. Helleri* but less umbonate.

Wet meadows and borders of streams, California and Arizona.

ANEMONE L. Anemone

Grains of two types, those with furrows and those with pores (*A. coronaria*). Grains with furrows oblately flattened, 20–28μ in diameter,

circular or somewhat triangular in outline, tricolpate. Furrows long, more or less tapering to broad rounded or jagged ends, their membranes conspicuously flecked with granules which resemble the papillae of the exine, their margins slightly roughened, jagged or fimbriate. Exine always conspicuously papillate, occasionally marked off into angular areas containing the papillae. These grains are similar to those of *Delphinium* but may be distinguished by their smaller size, flattened form and papillate exine.

The pored grains are similar to those of *Coptis* but may be distinguished from them by their larger size. Though these pored grains present a very different appearance from the furrowed grains of this genus, in reality they differ only in the number of their furrows, since the pores are morphologically merely reduced furrows; in all other respects they are the same as the furrowed grains of *Anemone*.

ANEMONE JAPONICA S. & Z. Japanese anemone. A large proportion of the grains abortive and variously irregular in shape. Normal grains oblate, rounded triangular in outline, 20.5μ in diameter. Furrows long, broad, and tapering to irregularly shaped ends, their membranes conspicuously flecked with rounded granules variously aggregated.

A stout branching plant with soft hairy basal leaves. Native of China and Japan, extensively cultivated elsewhere.

ANEMONE DEMISSA Hook. f. Grains similar to those of *A. japonica*, about 26μ in diameter. Furrows long, broad and tapering to symmetrically rounded ends, their membranes flecked with granules which may be separately dispersed or more or less arranged in striae, their margins nearly smooth, slightly roughened by the attachment to them of a few granules.

Himalaya.

ANEMONE DAVIDI Fr. Grains about 27.4μ in diameter. Furrows long and narrow, not greatly expanded at the center, their membranes flecked with scattered granules, their margins jagged.

These grains can be distinguished from those of the two preceding species by their narrower furrows with more jagged margins. In other respects they are similar.

Native of China.

ANEMONE VIRGINIANA L. Tall anemone. Grains 22.5–24μ in diameter. Furrow membranes flecked with granules which tend to coalesce in a central strip. Otherwise as in those of *A. Davidi*.

Common in woods in the eastern United States.

ANEMONE QUINQUEFOLIA L. Wind-flower, snow drops. Furrow membranes flecked with scattered granules, furrow margins jagged. Otherwise as in the grains of *A. virginiana*.

Native of eastern United States and Canada, closely resembling *A. nemorosa* which is native of Europe but cultivated in the United States.

ANEMONE CORONARIA L. Poppy anemone. Grains somewhat various, a large proportion obviously abortive, 22–32μ in diameter, spheroidal with about 15–18 pores which are variously irregular, sometimes elongate, but generally aproximately circular, their membranes heavily flecked with granules which tend to be aggregated towards the center, their margins rough. Exine rather thick and papillate as in other species of anemone.

The poppy anemone is native of the Mediterranean region, now a favorite hot-house plant cultivated in many varieties. The one from which the present specimen of pollen was obtained is known as "Craig Castle Improved."

PULSATILLA Adans. Pasque flower

Grains essentially as in *Anemone japonica*, 29–36μ in diameter, tricolpate or with supernumerary furrows. Furrow margins rough but not fimbriate. Exine rather thick, granular, and papillate.

The genus comprises about 18 species of perennial scapose herbs with thick root stocks, native of the north temperate and subarctic zones. In many classifications (e.g. Engler and Prantl) the group is regarded as a section of the genus *Anemone* to which it is undoubtedly closely related.

PULSATILLA HACKELII Pohl. Grains uniform 34–37μ in diameter, tricolpate.

PULSATILLA LUDOVICIANA Heller (*P. hirsutissima* Britt.). Grains various. 37.5–44.5μ in diameter, a large proportion with supernumerary furrows.

Plains and prairies. Almost throughout the United States and Canada west of Illinois.

PULSATILLA ALPINA Schrank. Grains extremely various, 29–33.5μ in diameter. Furrows generally more than three, a large proportion of the grains with 6, 12, and 15 furrows arranged according to the trischistoclasic system, others with furrows irregularly arranged.

SYNDESMON THALICTROIDES Hoffmg. (*Anemonella thalictroides* Spach.) Rue-anemone (fig. 5). Grains exceedingly various, 15–45μ in diameter. Furrows absent. Pores about 12–15, in the smaller grains circular, in the larger circular or variously irregular, their margins rough or jagged, more so in the larger grains. Exine rather thick, granular and papillate.

Normal grains of this pollen are of two sizes, exclusive of those which are obviously abortive. The larger are about 40μ in diameter while the smaller are about 20μ in diameter. The exine appears the same in both; it is of the same thickness, of the same granular nature and the papillae

which almost reach the proportions of spines, are of the same size. The result, however, is that the smaller grains appear to have a very thick and coarse exine. The number of pores in each bears no relation to the size of the grain; the smaller grains have the smaller pores so that the proportion of the surface occupied by pores is about the same in each. In the smaller grains, however, the pores are always approximately circular, while in the larger they may be elongate, even resembling ordinary furrows.

The genus comprises only this species, a low glabrous perennial herb, 4–9 inches high, resembling *Anemone quinquefolia*, with which it is often associated in woods throughout the eastern United States.

HEPATICA TRILOBA Chaix. Liver-leaf. Grains somewhat various, 28–30μ in diameter, oblate spheroidal, tricolpate. Furrows long narrow and tapering to jagged ends, their membranes rather thick and copiously flecked with papillae which tend to be aggregated in a band in the center of the furrow like a central strip of exine. Furrow margins rough or jagged, often with adhering flecks of the furrow membrane.

Native of eastern United States and Canada, also in Europe, Alaska and Asia.

CLEMATIS L. Clematis

Grains oblately flattened and rounded triangular in outline or spheroidal, 19–25.5μ in diameter, tricolpate, occasionally otherwise. Furrows long and tapering, their membranes more or less copiously flecked with coarse granules variously aggregated, their margins smooth or jagged, generally with strands or clusters of the membrane granules adhering. Exine rather thick, conspicuously papillate. Intine thick and further thickened beneath the furrows.

Climbing vines more or less woody, with cymose paniculate flowers. About 25 species of cosmopolitan distribution.

CLEMATIS MONTANA Buch.-Ham. (fig. 6). Grains various, a large proportion abortive. Normal grains oblate, rounded triangular in outline, 19–25.5μ in diameter. Furrows long and tapering to rounded ends, their membranes only sparsely flecked.

A tall climber, reaching 15–20 ft. Native of Himalaya, cultivated elsewhere.

CLEMATIS PICKERINGII Gray. Grains spheroidal, about 22.8μ in diameter. Furrow membranes densely covered with papillae rendering them scarcely distinguishable from the exine. Otherwise as in *C. montana*.

NARAVELIA ZEYLANICA DC. Grains uniform, 17–19μ in diameter. Furrows absent. Pores about 15, approximately circular, their membranes

thick and densely flecked with granules rendering them similar in appearance to the exine. Exine rather thick, finely but conspicuously granular.

These grains resemble those of *Coptis* and *Synedesmon* but may be distinguished by their granular instead of papillate exine. They also resemble those of *Thalictrum* but may be distinguished by their smaller size. In their tendency towards obliteration of the pores they resemble those of some species of *Alisma*.

Perennial climber, native of Malaya.

MYOSURUS MINIMUS L. Mouse-tail. Grains uniform, spheroidal, about 20μ in diameter, tricolpate. Furrows long broad and tapering to jagged ends, their membranes flecked with granules resembling the papillae of the exine, their margins jagged. Exine rather thin, papillate. Intine thin but thickened beneath the furrows.

A low annual with linear-spatulate leaves and naked one-flowered scapes. Native of the central and southern parts of the United States, and Europe. The genus contains about 5 species principally of North America.

TRAUTVETTERIA GRANDIS Nutt. False bugbane. Grains uniform, about 25μ in diameter, tricolpate, occasionally some grains otherwise. Furrows long and narrow, scarcely tapering to irregularly shaped ends, their membranes copiously flecked and margins fimbriate, both to such an extent that the furrows are nearly obliterated. Exine rather thick, papillate, faintly marked off into angular areas enclosing the papillae.

A perennial herb with palmately lobed leaves and corymbose white flowers, resembling *Cimicifuga*, apparently partly adapted to wind pollination. British Columbia to California and eastward to Montana; eastern Asia. The genus comprises only this species.

OXYGRAPHIS CYMBALARIA Prantl (*Ranunculus Cymbalaria* Pursh, *Halerpestes Cymbalaria* Greene). Seaside crowfoot. Grains spheroidal, 19–20.5μ in diameter, tricolpate. Furrows long and tapering, their membranes heavily flecked, their margins not sharply defined, the texture of the furrow membranes merging with that of the general exine. Exine papillate. Intine thin.

Low glabrous herb with mostly basal cordate leaves, spreading by runners. On sandy shores, northeastern United States and Canada. The genus comprises about 9 species in central and eastern Asia, and North America, frequently regarded as a section of the genus *Ranunculus*.

RANUNCULUS Tourn. Crowfoot, buttercup

Grains spheroidal or oblately flattened, about 22–32μ in diameter, tricolpate, occasional grains tetra- and hexacolpate or variously irregular. Furrows long and tapering to broadly rounded ends, their membranes

flecked with conspicuous granules, their margins jagged or fimbriate. Exine thin, papillate.

The genus comprises more than 200 species of low terrestrial or aquatic herbs of wide distribution.

RANUNCULUS ABORTIVUS L. Small-flowered buttercup (fig. 7). Grains mostly normal 22.5–26.5μ in diameter.

Woods and moist places almost throughout the United States and Canada east of the Rocky Mountains.

RANUNCULUS ACRIS L. Tall crowfoot, buttercup. Grains mostly with supernumerary furrows, short with rounded ends, their membranes copiously flecked, 26–32μ in diameter.

Almost throughout Europe and North America.

RANUNCULUS PURSHII Richards. Grains similar to those of *R. abortivus*, about 30μ in diameter.

A glabrous aquatic herb with filiformly dissected leaves, wholly immersed or creeping on muddy banks. Throughout northern United States and Canada.

BATRACHIUM Water crowfoot

Grains essentially as in *Ranunculus*, tricolpate or with six or more furrows, the latter broad and tapering to rounded or jagged ends, their membranes conspicuously flecked. Exine thin papillate. Intine thin and not thickened beneath the furrows.

Aquatic perennials with immersed disected leaves and aerial flowers. Closely related to *Ranunculus*.

BATRACHIUM CONFERVOIDES Fries. (*Ranunculus aquatilis* L.). Grains uniform, about 27μ in diameter, tricolpate.

Common, especially in slow-flowing streams almost throughout the United States and Canada.

BATRACHIUM sp. Grains uniform in size, 36.4–37.7μ in diameter. Furrows more than three, irregular in arrangement but mostly representing imperfectly the configurations of the trischistoclasic system.

THALICTRUM Tourn. Meadow-rue

Grains spheroidal, of various size from 18 to over 30μ in diameter, without furrows but provided with 7–18 pores, the latter approximately circular, their membranes flecked with coarse granules, sometimes so copiously as to be almost obliterated by them, their margins smooth or with adhering granules. Exine finely but conspicuously granular.

These grains are similar to those of *Naravelia* but may be distinguished by their generally larger size and fewer pores.

The genus comprises about 76 species of slender branching herbs with ternately compound leaves and wind-pollinated flowers. Widely distributed in Europe, Asia, and America.

THALICTRUM DIOICUM L. Early meadow-rue (fig. 8). Grains uniform, about 18.5μ in diameter. Pores 6–10, prevailingly, 6, tetrahedrally arranged their membranes heavily flecked.

A slender herb of moist woods, common in the northeastern United States and Canada.

THALICTRUM POLYGAMUM Muhl. Tall meadow-rue. Grains uniform, 22.5–25.5μ in diameter. Pores 7–9, various in size, circular or elongate in outline, when the latter occasionally triconvergent, their arrangement resembling that of furrows in the trischistoclasic system.

Native of the eastern United States and Canada.

THALICTRUM CLAVATUM DC. Grains extremely various; many of them dwarfed and obviously abortive. Normal grains about 28.5μ in diameter, but many apparently normal both larger and smaller. Pores about 15–18, uniform, their membranes copiously flecked.

Similar in appearance to early meadow-rue but flowers white and all perfect. Native of the eastern half of the United States, principally southward.

THALICTRUM DIPTEROCARPUM Franch. Grains somewhat various, 17–23.8μ in diameter. Pores 10–12, various, their number not correlated with their size or with that of the grain.

ADONIS [Dill.] L. Adonis

Grains generally uniform, ellipsoidal or spheroidal, 25–30μ in diameter, tricolpate. Furrows long and narrow, tapering to pointed or blunt ends, their membranes copiously flecked or encrusted with material resembling fragments of the exine, their margins rough. Exine thick and rigid, granular and slightly papillate.

Annual or perennial herbs with finely dissected alternate leaves and showy flowers.

Native of north temperate regions of Asia and Europe.

ADONIS AESTIVALIS L. Summer adonis. Grains ellipsoidal, deeply three lobed in outline with the furrows in the depressions. Furrows narrow, tapering to sharply pointed ends, their membranes heavily encrusted with a longitudinal strip of material resembling coarse-textured exine, almost completely demobilized. Exine finely granular and vaguely papillate, rather thick throughout and greatly thickened at the poles (umbonate).

The elongate form of these grains, which is generally maintained even when fully expanded, is due to the nearly complete demobilization of the furrows.

A commonly cultivated herbaceous perennial. Native of central Europe.

ADONIS VERNALIS L. Spring adonis. Grains uniform, spheroidal or slightly ellipsoidal, not three lobed. Furrows tapering to blunt ends, their membranes copiously flecked, but not heavily encrusted. Exine fine-granular, finely but distinctly papillate, thick but not further thickened at the poles (not umbonate).

These grains differ from those of *A. aestivalis* principally in the lack of encrustation of the furrow membranes, and the lack of umbonate thickenings at the poles.

A commonly cultivated herbaceous perennial, native of central and southeastern Europe.

While this paper was in the hands of the publisher there appeared an article on the same subject (Kumazawa, M. 1936). It is unfortunate that this work came to my notice too late to receive adequate consideration, since the author describes and illustrates the pollen grains of many of the species treated here. Dr. Kumazawa's findings and mine are substantially in agreement; particularly noteworthy is this author's conclusion that the pores of the pored grains represent proliferated and shortened furrows.

Yonkers, N. Y.

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Explanation of plate 20

Fig. 1. Pollen grain of *Paeonia albiflora*, approximately in polar view, 34μ in diameter.

Fig. 2. Pollen grain of *Caltha palustris*, approximately in polar view, 25μ in diameter.

Fig. 3. Pollen grain of *Coptis trifolia*, 18μ in diameter.

Fig. 4. Pollen grain of *Aconitum delphinifolium*, approximately in polar view, 25μ in diameter.

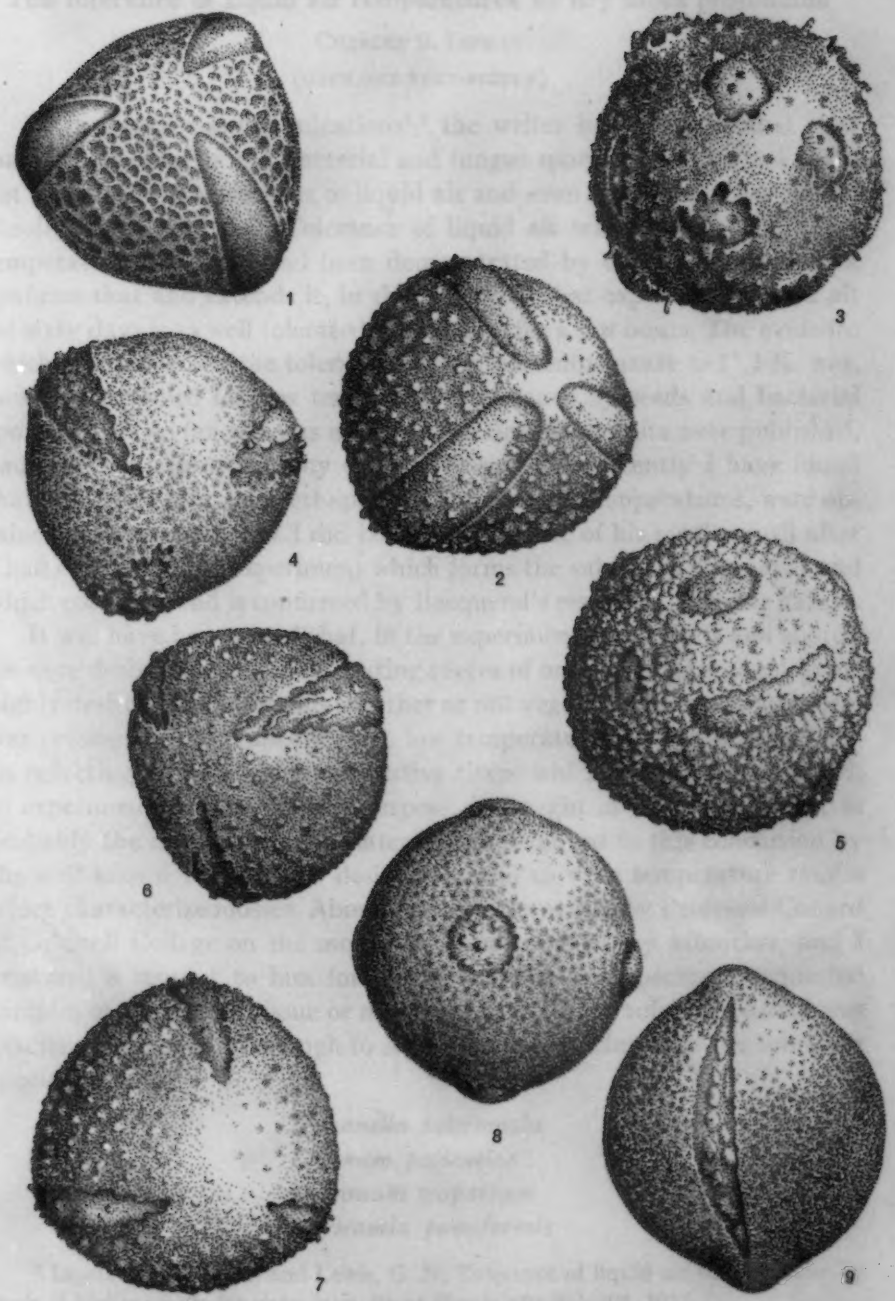
Fig. 5. Pollen grain of *Syndesmon thalictroides*, 40μ in diameter.

Fig. 6. Pollen grain of *Clematis montana*, approximately in polar view, 22μ in diameter.

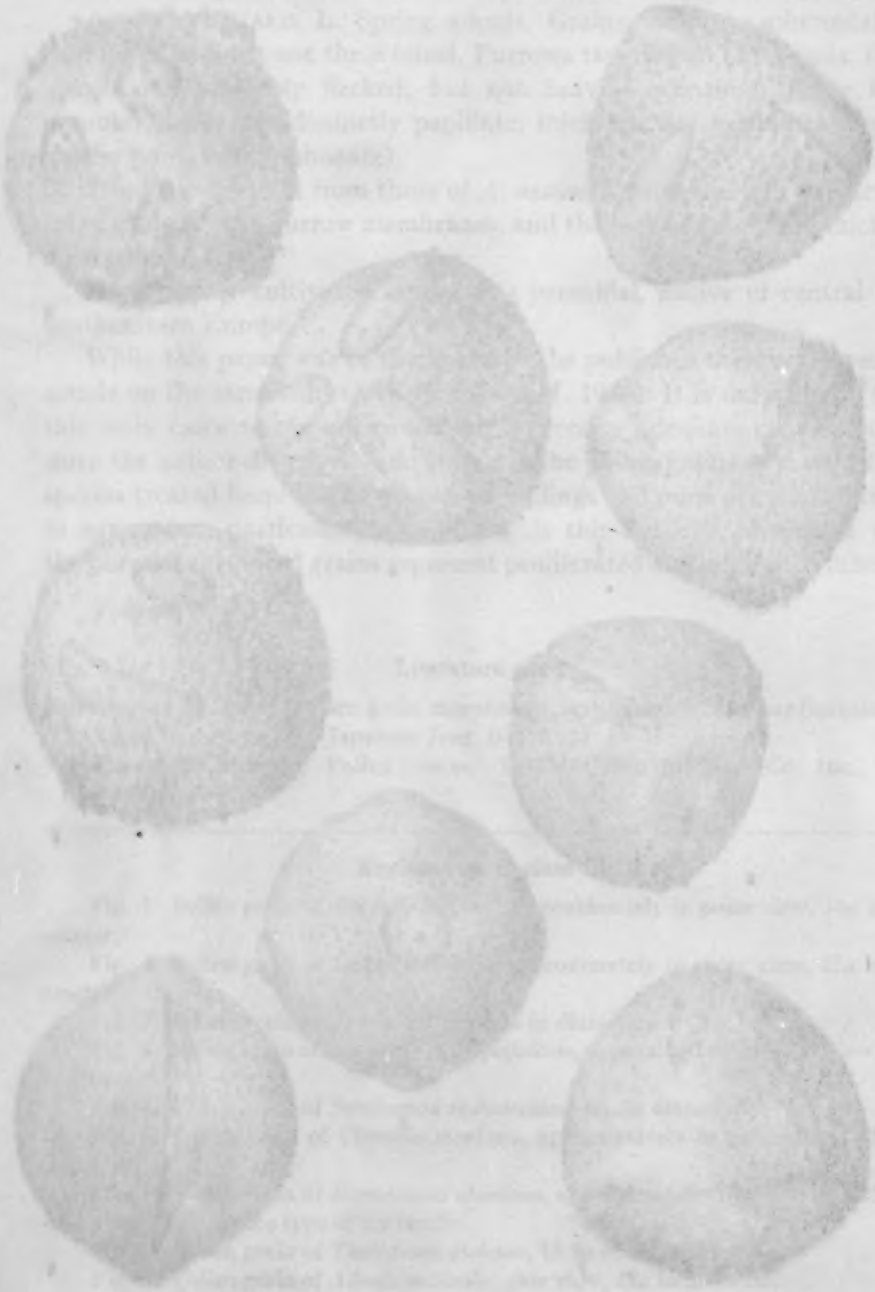
Fig. 7. Pollen grain of *Ranunculus abortivus*, approximately in polar view, 25μ in diameter, chosen as the type of the family.

Fig. 8. Pollen grain of *Thalictrum dioicum*, 18.5μ in diameter.

Fig. 9. Pollen grain of *Adonis aestivalis*, side view, 28μ in diameter.



WODEHOUSE: POLLEN OF RANUNCULACEAE



The tolerance of liquid air temperatures by dry moss protonema

CHARLES B. LIPMAN

(WITH ONE TEXT-FIGURE)

In two earlier communications[1,2] the writer has demonstrated that many kinds of seeds and bacterial and fungus spores can withstand without injury the temperatures of liquid air and even those very close to the absolute zero (1°.3 K.). Tolerance of liquid air temperatures and lower temperatures by seeds had been demonstrated by others, and my work confirms that and extends it, in that I proved that exposure to liquid air for sixty days is as well tolerated as exposure for a few hours. The evidence which I presented on the tolerance of so low a temperature as 1°.3 K. was, however, a record for low temperature tolerance by seeds and bacterial spores which, so far as I was aware at the time the results were published, had not been approached by other investigators. Recently I have found that similar results, but perhaps at slightly higher temperatures, were obtained by Becquerel, but I did not become aware of his results until after I had completed the experiment which forms the subject of this paper and which confirms, and is confirmed by Becquerel's results of a similar nature.

It will have been noted that, in the experiments with seeds and spores, we were dealing entirely with resting stages of organisms. It seemed to me highly desirable to determine whether or not vegetative tissue in any form was possessed of tolerance to such low temperatures as that of liquid air. In reflecting on the kind of vegetative tissue which might lend itself well to experimentation for such a purpose, I thought of moss protonema as probably the most promising material. I was moved to this conclusion by the well-known tolerance to desiccation and to wide temperature ranges which characterize mosses. About that time an article by Professor Conard of Grinnell College on the mosses of Iowa came to my attention, and I ventured a request to him for samples of different species. I requested samples of vegetative tissue or non-fruiting species. Professor Conard was gracious and generous enough to send me small specimens of the following species of mosses:

Dicranella heteromala
Hypnum patientiae
Dicranum scoparium
Bartramia pomiformis

[1] Lipman, Charles B., and Lewis, G. N. Tolerance of liquid air temperatures by seeds of higher plants for sixty days. Plant Physiol. 9: 392–394. 1934.

[2] Lipman, Charles B. Normal viability of seeds and bacterial spores after exposure to temperatures near the absolute zero. Plant Physiol. 11: 201–205. 1936.

Thelia asprella
Entodon seductrix
Brachythecium cytrophyllum
Catharinea angustata

Professor Conard stated that *Hypnum patientiae* and *Entodon seductrix* never fruit in Iowa, and that the others showed no signs of fruiting when the specimens were collected. They were all collected nine miles southwest of Grinnell, Iowa, in Jasper County.

Fig. 1. Photograph of three of the treated mosses and controls. Reading from left to right:

Hypnum patientiae
Thelia asprella
Brachythecium cyrtophyllum

Top row control specimens, only dried in vacuum. Lower row treated specimens, fifty hours in liquid air. Specimens all growing in soil in tumblers.

The specimens reached me on October 8, 1935. Being occupied at the time, I set the specimens aside in the dry condition in which they arrived in tissue wrappings. They remained thus until December 26, 1935, when they were placed in a desiccator over sulphuric acid, and the desiccator was evacuated. The specimens remained in this dry vacuum until February 14, 1936, when they were removed and treated as follows: Each specimen, though very small (about half an inch to an inch in diameter) was

divided into two. One of the halves was placed in a Pyrex tube, and the tube was sealed. The other half was saved for a control. The samples of the different species thus prepared in sealed tubes were immersed in liquid air and kept there for fifty hours (temperature approximately −190° C.). At the end of fifty hours the specimens were removed from the sealed tubes, and each was placed in a beaker of tap water. The controls were likewise placed in beakers of tap water. All the specimens remained in the beakers from February 20–24, 1936. Within a few hours it was evident that all the moss specimens, both the controls and treated, had swelled markedly, and microscopic or other examination showed the cells to be perfectly normal, the chloroplasts in good condtion, and apparently none the worse for the long and very rigorous drying, or the liquid air exposures in the case of the treated samples. After four days in the tap water, the mosses were removed to the surface of moist and properly prepared soil in tumblers. Fungi had attacked them all in the tap water, and some of the samples were beginning to disintegrate. In spite of that, three of the eight species survived the attacks of the fungi, and are growing very well to this day (July 15, 1936). A photograph showing control and treated specimens of these three species accompanies this paper. The other species were so injured by fungus attack that they died. It will be noted that the controls, as well as the treated specimens, died in this manner. It is fortunate that one of the species which survived the attacks of the fungi was *Hypnum patientiae*, which, as Professor Conard reports, never fruits in Iowa. There can certainly be no question of surviving spores, in this case, having been responsible for the growth obtained.

The foregoing experiment leaves no doubt that the protonema of moss in a dry state can withstand the temperature of liquid air as well as seeds do, and as well as spores of bacteria and fungi, as the writer in common with others, proved earlier. An examination of the photograph which accompanies this paper will satisfy the reader that the mosses treated, as well as untreated, are growing actively and producing new and healthy shoots. I stated above that, after I had completed this experiment, there came to my attention the recent work of Becquerel, which my experiment confirms. I did not learn of the report of Becquerel's work on mosses, in very brief form, until I saw the Proceedings of the Sixth International Congress of Cryoscopy held at Buenos Aires in September, 1932. Soon thereafter, I learned of Becquerel's report to the International Botanical Congress held at Amsterdam in September, 1935, which in the Proceedings of that Congress gives another very brief account of experiments with seeds and spores near the absolute zero, but does not mention any further work with dried vegetative tissue. I shall have occasion to refer, in another

paper bearing on related experiments, to other phases of Becquerel's work and to experiments of others of a most striking nature. It is pertinent in this connection, however, only to point out that Becquerel's work on mosses and mine are mutually confirmatory. Moreover, Becquerel's generalization from his experiment with mosses and from his other low temperature experiments, relative to the absence of respiration in organisms kept at very low temperatures, is in entire agreement with my own. Several years ago in a paper read before the National Academy of Sciences at a meeting held in Berkeley, I gave an account of my discovery of living bacteria in anthracite coal, in which I stated as one conclusion my belief that spores of bacteria might exist in rocks or in other old forms of matter in a non-respiring state which I called "suspended animation." In my papers to which I referred above, I gave the definite proof of the correctness of my earlier conclusion. I find now that in the brief account of Becquerel's discussion before the International Botanical Congress at Amsterdam, he uses exactly the same term as I used several years ago. It is gratifying to me to have arrived quite independently at the same conclusion as Becquerel respecting this important matter. Since I shall have more to say elsewhere on "suspended animation," I need say nothing further about it here, except that moss protonema can apparently stop respiring without losing its power to live at some later time under the proper conditions, just as several of us have proved that seeds and spores can do, and this further emphasizes the correctness of my conclusion that the property of life depends not on a reaction, but on a pattern or design of matter. It is unthinkable that respiration can go on either at liquid air temperatures or at the absolute zero, when all the materials and conditions necessary to respiration are effectively absent.

To Professor H. S. Conard of Grinnell College, who furnished the moss specimens for this experiment, to Professor C. W. Porter of the Chemistry Department of the University of California, who supplied the liquid air therefor, and to Mr. W. L. Chandler, who assisted me with the laboratory work, I acknowledge my grateful indebtedness.

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An international system of botanical districts[1]

CARL O. GRASSL

My interest in plant geography has convinced me that if we are to advance efficiently in this science it will be necessary to standardize our main concepts and procedures. With this idea in mind I am proposing for the consideration of collectors and herbarium students some innovations in the manner of recording phytogeographic data.

The crying need for a serviceable subdivision of the earth's surface into botanical districts leads me to suggest that we make use of small quadrangles limited by meridians and parallels, the unit botanical district to be a square degree. In other words, the areas bounded by whole degrees of latitude and longitude should be recognized as botanical districts.

Such a system of botanical districts would divide the surface of the earth into 64,800 distinct rectangular units one degree on a side. Actually we would not be very much concerned with many of these, as much of the earth is covered by oceans or ice-fields on which, for the most part, plants are not to be expected. A rough estimate indicates that about twenty thousand of these areas play a part in the distribution of the higher plants. That twenty thousand or so unit districts is not an unreasonable number will, I hope, become clearer as the advantages of the system are pointed out.

In order to facilitate the comparison of the proposed system with any others that may come to mind, I have listed the main reasons that have led me to believe this system the best. The reasons dealt with below, are not necessarily in the order of their importance.

CONVENIENCE AND SIMPLICITY OF THE UNIT

A "square degree," the unit of the proposed system of botanical districts, can be represented in a manner which is very convenient and yet be immediately understandable to all students of science throughout the world. For example, the district in which Ann Arbor, Michigan, is situated might be represented thus: 42-3N83-4W, meaning the area between 42° and 43° North Latitude, and between 83° and 84° West Longitude. This short way of designating a district could be even more abbreviated, i.e., to 42N83W, if it was understood that an area was meant rather than a point. For most purposes the slightly longer but customary way of indicating an area is preferable.

The areas represented by quadrangles of a square degree are reason-

[1] Papers from the Department of Botany and Herbarium of the University of Michigan, No. 593.

ably uniform in size and shape. The only appreciable variation that occurs is in longitude as one goes towards the poles. This is because a degree of longitude varies from about 70 miles at the equator to zero at the poles. Inasmuch as this variation is in width only (the variation in latitude being less than 1%) and since it is not appreciable between neighboring units; it can for most purposes be disregarded. This is especially true since the districts which are most affected lie near the poles and consequently do not concern us very much. In studies where it is desirable to compare equal areas which are widely separated in latitude, such as arctic regions with tropical ones, it is only necessary to make use of the flexibility of the system as indicated below. For example several neighboring arctic districts could be lumped together thus: 81-2N45-8W, to obtain an area almost equal to a single unit near the equator.

The areas which these districts represent are of a convenient size. An average district will be about 50 miles wide and 69 miles long. Another way of realizing their size is to consider that the United States contains about 900 such units. The size of these units is convenient because it is large enough so that the areas may easily be found on small scale maps and yet is small enough to serve as a basis for local floristic studies.

The principal advantage of having such uniform and therefore comparable districts is that it will simplify treating the major problems of plant distribution. As soon as we possess data for numerous comparable units it becomes a simple matter to recognize similarities and differences between them and from these to draw valuable conclusions. Uniform units will enable us to construct zones of vegetation which are actually based upon the complex of plant distribution rather than as at present, upon compromises and guesswork. In other words, the use of a fundamental unit is necessary for precision in the comparison and subordination of phytogeographic data.

FLEXIBILITY OF THE SYSTEM

A system of districts based upon meridians and parallels, and having as its unit a square degree, has the great advantage of being flexible, inasmuch as areas of a larger or smaller size are readily formed by grouping or subdividing them. The ways in which this could be utilized are numerous and important, and consequently will be dealt with in some detail.

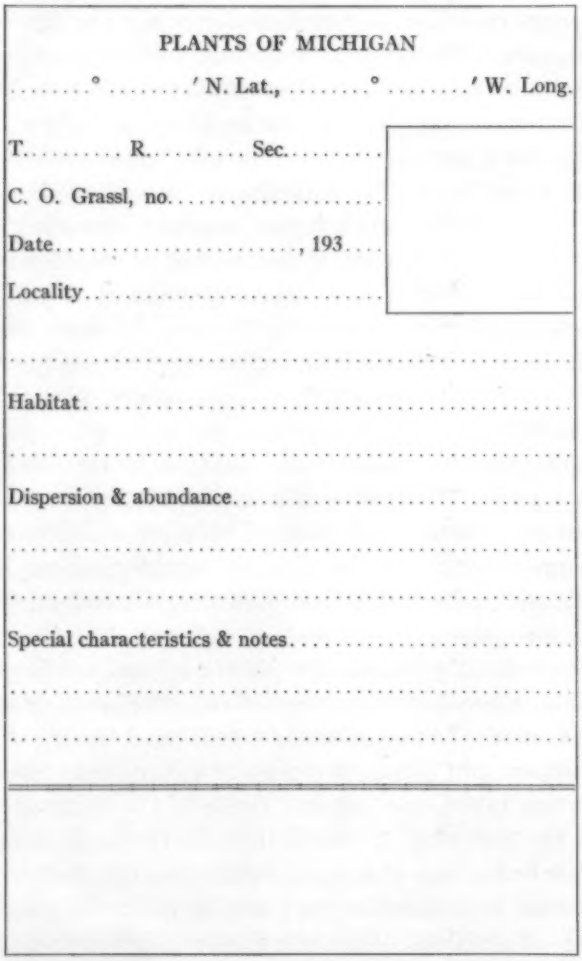
Starting with the subdivisions, we find that the most important and usable modification would be the addition of minutes of degree as a means of indicating the approximate locality at which a collection was made. This would fit in excellently with the above system of districts as it would enable us to change at will the size of the units upon which we were basing

our distribution studies. Application of this modification appears imminent as it is becoming more obvious every day that locality references, if they are to be usable, must be qualified by degrees and minutes of latitude and longitude.

The question as to how plant localities should be recorded on the labels of plant collections and in floristic and monographic reports is becoming more important with every increase in the number of collections and in the accuracy with which they are localized. A satisfactory solution to this problem must take into consideration various factors. To be successful, a method of recording plant localities must not only be practical as far as the collector is concerned, and therefore based upon the best maps available, but must be readily understandable and usable by museum students. Undoubtedly the most logical and satisfactory method of accomplishing this is by qualifying, in terms of degrees and minutes of latitude and longitude rather than in terms of political units, the exact locality at which a collection was made. This would mean that instead of saying that a collection was made at a given spot, at a given distance and direction from a recognizable city, in a given county, of a given state, we would stress and improve the accuracy of the information about the exact locality, and describe its approximate position in terms of the nearest meridian and parallel. The growth of cities, and the frequent changes and duplications in place names and political units, makes any system based upon them temporary and provincial if not actually impracticable.

It would be well indeed, if we could localize our collections even more accurately, as for instance, to seconds of a degree; but since our present maps do not permit this, localization has to be realized in another way. To find (probably many years later) practically the identical spot at which a collection was made, I have designed a field label (see fig. 1) with a rectangle in the upper right corner to represent a map of the area from which the collection was taken, the size and shape of the rectangle determined by the grid of the base map. If practicable, the rectangle should represent a square minute or fraction of a minute of degree. Generally, however, the rectangle will have to be based upon a map in which the subdivisions represent public-land divisions. Whatever the rectangle represents should be indicated upon the field label. In figure 1, the rectangle (in this instance a square) represents a public-land division of one square mile in extent known as a section and commonly shown on United States topographic and soil maps. Suitable blank spaces in which to indicate which section is meant and the township (distinguished by township and range numbers rather than by name) in which it occurs have been provided on the label. By carefully marking the square not only can we indicate (with an error

of only a few hundred feet) the spot at which a collection is made, but also the distribution of the species with respect to the topography, soil, and other edaphic factors. A triangle could be used to designate the spot at which the collection was made, while plus and minus signs could be used to indicate the presence or absence of the species as far as the observations


PLANTS OF MICHIGAN

..... ° ..... ′ N. Lat., ... ° ..... ′ W. Long.

T..... R..... Sec.....

C. O. Grassl, no.....

Date....., 193....

Locality.....

.....

Habitat.....

.....

Dispersion & abundance.....

.....

.....

Special characteristics & notes.....

.....

.....

Fig. 1. A field label for use in the United States. The square in the upper right corner represents a section (one square mile). Actual size 5 by 3 inches.

permitted. It is only by some such method that collectors can prepare collections with permanent phytogeographic as well as taxonomic significance.

I have purposely planned a small label (5 by 3 inches) so that a pad of them may conveniently fit into one's pocket and also so that they may

serve in emergency as ordinary herbarium labels. When it is desirable to take more copious notes than the few blank lines allow it is only necessary to use the back of a second label. If one wishes a separate herbarium label the field label can be shortened to 4 inches by eliminating the space for the Latin name.

It is unfortunate that so few collectors use field labels. As E. D. Merrill[2] has often pointed out, there can generally be no serious objection to the use of field labels. On the contrary, they enable the conscientious collector to work much more efficiently and accurately than is possible without them. Probably the main reason why many collectors avoid the use of field labels is their inability to apply them to the outmoded ways of collecting with a vasculum or some similar equipment. Why anyone should use a vasculum when many more and much better specimens can be obtained by collecting directly into a press (with shoulder straps if so desired) is not understandable.

The expense of field labels is not a valid objection to using them, for it is better to retain a field label as a permanent herbarium label than it is to dispense with a field label because generally more expensive herbarium labels are to be printed later.

Returning to the uses of subdivisions, it would turn out that students in the relatively more botanized districts, such as the New England States, would find a square degree too large a unit. Then $\frac{1}{4}$ or 1/16 of a square degree would be a convenient area on which to base local studies, since topographic maps at least in the United States are prepared, for the most part, on that basis.

When we consider the many possible ways of combining degree units to form larger areas we find many more advantages to our system. Regions of five or ten degrees on a side might very well be considered as suitable areas for more comprehensive floristic work. Such groupings could be made much more natural and comparable than the political ones now used.

Another way in which large aggregates of unit districts could be made use of is in the segregation of herbarium sheets. For this purpose there are any number of possible arrangements all based upon the same principles of numerical progression in longitude and latitude. The size of the steps of latitude and longitude used for each folder could be based upon the range and abundance of particular species. Within the folders representing the major groupings any degree of refinement in arranging the sheets could be accomplished. Some such system would greatly facilitate her-

[2] Merrill, E. D. On the utility of field labels in herbarium practice. Science, N.S., **44**: 664–670, 1916. The significance of the compiler's data in field work. Bull. Torrey Club, **61**: 71–74, 1934.

barium research and would eventually be practicable if some of the other suggestions made above were ever realized.[3]

Still another use for such districting as I have suggested would occur whenever accurate regional bibliographies or abstracts of regional reports were to be prepared. The ease with which meridians and parallels could be used to indicate and index the exact regional significance of a report would greatly simplify bibliographical problems.

INTERNATIONAL IN SCOPE

Finally we have the fact that districts based upon meridians and parallels have permanent boundaries and are international in scope. This will greatly aid us in the tremendously important work of accurately mapping the distribution of species throughout the world. Because of the great regularity exhibited by districts of a square degree, uniformity in the manner of mapping will be relatively easy to accomplish. Uniformity in the manner of mapping the distribution of species can be further increased, by setting up suitable criteria based upon the number of distinct stations and their position within the districts.

It is unfortunately true that, in spite of the fact that the meridian of Greenwich has been universally accepted as the initial meridian, most topographic maps of foreign countries are still based upon local meridians. The Portuguese, for example, use the meridian of the Naval Observatory in the Royal Park at Lisbon (9°11′10″ West of Greenwich). This is not an important obstacle, however, as it is very easy to change a longitude so that it is based upon Greenwich. A collector in Portugal would only have to add 9°11′10″ to each longitude to base it upon Greenwich. If on the other hand one was collecting in France, it would only be necessary to subtract 2° 20′14″, since Paris (Obs. nationale) 2°20′14″ East of Greenwich is there used as the prime meridian. In a similar manner allowance could be made for any local meridian now in use.

Summing up the arguments for a system of botanical districts based upon the square degree we find that it would be advisable because of its simplicity, flexibility, and practicability. Evidence indicating its workableness has been obtained in the field and herbarium study for a report that I am preparing on plant distribution in the northern Great Lakes Region.

DEPARTMENT OF BOTANY
UNIVERSITY OF MICHIGAN

[3] For other ways in which botanical districts of a square degree can be made use of in herbaria see the writer's article "Visualizing our herbaria by the application of mechanical methods of tabulating and indexing." Museums Journ. (in press).

On the classification of Euphorbia. I. How important is the cyathium?

LEON CROIZAT

A century and a half of controversy has left it undecided whether *Euphorbia* L. is a single genus or a group of genera. The quarrel of the Linneists and Anti-Linneists[1] has been fought to a standstill, with the Linneists at present more numerous. In itself the issue is older: its roots are in the works of the herbalists who saw a distinction, rejected by Linnaeus in all his works, between *Chamaesyce* and *Tithymalus*, *Euphorbium* and *Peplis*.

As presented by either school the classification of *Euphorbia* or of the genera segregated from it challenges an impartial observer. The Linneist stands by a generic definition two centuries old which assumed that the cyathium is a flower. The major premise of this definition has been proved false: the cyathium is an *inflorescence, not a flower*. One must wonder whether a notion fundamentally erroneous can become fundamentally true. Furthermore, the Linneists too easily surrender the right to understand and to interpret facts that bear vitally upon classification. Says Boissier (D.C. Prodr. **15**[2]: 8. 1862), "The characters of the sections are often trifling and open to exception but *better ones can not be found*" (translation and italics mine). N. E. Brown writes (Fl. Trop. Afr. **6**[1]: 471. 1911), "The spines of succulent species in books have been called 'stipular spines', but as they are always developed below, and sometimes at a distance below the leaf or the leaf-scar, they cannot be stipules in the ordinary sense of that term; *what their real relation to the leaf is I do not quite understand*" (italics mine). No one familiar with these and like statements feels surprised in finding that the "sections" of *Euphorbia* are *nomina nuda* or without precise definitions. In fact the same "section" includes species with or without "stipules," with or without a definite main axis, and with or without a terminal inflorescence, and digests without difficulty species that are glaringly unrelated. However, such "sections" are a lesser evil than the blank classification of some Linneists. The works of these taxonomists scarcely exceed the value of a catalogue or of a collection of descriptions; their secrets are sealed except to the peering eye of profound hierophants.

The classification of the Anti-Linneists is fundamentally negative. It repudiates as a matter of course the "unnatural union of the spotted

[1] By "Linneists" are here understood the botanists who believe *Euphorbia* L. to be a single genus, by "Anti-Linneists" those who take the contrary view. The terms are used for brevity, and are not derogatory.

spurge and of the garden caper" (Eaton, Man. ed. 2. 243. 1818), but seems incapable of producing generic definitions that precisely apply to one harmonious group of species and interpret the structures that puzzle the Linneists. The weakness of the Anti-Linneistic definitions is trifling compared with the tendency inherent in the concepts of the school to introduce monotypic genera based upon the study of a limited flora. Nothing is gained in the adoption of principles that segregate one species from two thousand.

Both systems of classification, then, are stultified by a hidden inconsistency, and blighted by a false start. If the definitions of the genus and of the genera are unsatisfactory the trouble plainly lies in the concepts.

The Linneists and the Anti-Linneists appear to differ fundamentally in this: The Linneists believe that cyathium and *Euphorbia* are synonymous, or very nearly so, and refuse to admit the validity of differences in habit, spines, stipules, and the like. Their position, bluntly stated, is one of conservatism hallowed by tradition. The Anti-Linneists lay stress on the differences in habit, spines, sizes, stipules and the like, and claim that these differences are weightier than the mere possession of a cyathium. Their position is difficult, for they must produce proofs and overcome the authority of standing classification.

We have defined the issues. Let us, this being done, take the concepts of the opposing schools and reduce them to their fundamental thesis. We hear:

a) The cyathium is not *the* generic character of *Euphorbia*.

b) the cyathium is *the* generic character of *Euphorbia*.

From 1870 on all botanists have agreed that the cyathium is an inflorescence. Accordingly we substitute equivalents, and have;

a′) the inflorescence is not *the* generic character of *Euphorbia*.

b′) the inflorescence is *the* generic character of *Euphorbia*.

The substitution of *inflorescence* for *cyathium* takes the issue out of the narrow circle of the "specialists" and brings it for a verdict to the common run of botanists who all know how *inflorescences* are treated in taxonomy. Five questions follow.

The first question is addressed to the Anti-Linneists: what in their concept, is the generic character of the various groups of species they segregate from *Euphorbia?*

The answers are many and should be analyzed in detail, were not this paper concerned with principles. The Anti-Linneists more or less soberly agree that the cyathium is important in its parts if not as a whole: they postulate appendages, glands, seeds, and to a lesser extent, perhaps, "stipules" and phyllotaxis. If the writer be correct, Ch. Lemaire single-

handed proposes a concept that is reminiscent of the evolutive interpretation of groups of species (cfr. Observations on *Anthacantha*, Ill. Hort. **2:** Misc. 68, 1855; **5:** Misc. 64, 1858). It is evident that most if not all of the Anti-Linneists still believe in the cyathium, and wage mere verbal warfare against the Linneists. C. F. Millspaugh, a name to conjure with in certain parts of the world, undoubtedly has much in common with Rafinesque, at least with Rafinesque in a sober mood, and there is a suspicion that the extreme conservatism of many an American taxonomist expresses a psychological reaction to the Rafinesquian and Millspaughian serenades. Klotzsch is vastly more ambitious than Necker but not better informed; Boissier castigated him, and the botanists of Europe, mayhaps, still fear the shadow from Geneva.

The Linneists are positive or very nearly positive that where there is a cyathium there stands *Euphorbia*. Their position is clear, and invites precise questions. Three will be asked of them:

1st) Does the inflorescence of *Euphorbia* belong to a group of species that are alike in degree of evolution?

The answer is no. Some species have interpetiolar stipules, others glandular stipules; some are annual, unarmed herbs with opposite leaves, others biaculeate perennial trees with reduced alternate leaves. The "spines" result from spinescent branches as in *E. lignosa* and *E. triaculeata*, from dried persistent floral peduncles as in *E. polygona*, from the operation of a process to most authors wholly unintelligible as in *E. antiquorum* and *E. Cooperi*. Beyond these differences, furthermore, the Linneist recognizes a fundamental likeness among the species of certain groups. Hence the "sections," and the admission that, after all, an *Anisophyllum* is not a *Tithymalus*, even though a *Trichosterigma* may be anything having "petaloid" appendages, and *Goniostema* can nurse on its capacious bosom half the species of Madagascar.

2nd) Does the inflorescence of *Euphorbia* L. belong to that genus alone?

The answer is no. An inflorescence in which certain members (bracts or scales) become adnate to form an involucre for the flowers, basically a cyathium, belongs to at least seven genera that are accepted in the seats of orthodoxy, and to fifty or more genera devoutly believed in by less orthodox botanists. Pax, whose concepts coincide with those of Engler's Pflanzenreich and may not be suspected of heterodoxy, rejects *Pleuradena* (*Poinsettia*) but indorses *Diplocyathium*, *Anthostema*, *Dichostema*, *Calycopeplus*, *Euphorbia*, *Elaeophorbia*, *Synadenium*, *Monadenium*, *Stenadenium*, and, it seems, *Tithymalus* (*Pedilanthus*). Pax states that the cyathium is the main character of *Euphorbieae*, not of *Euphorbia* (Bot. Jahrb. **59:** 151, 1924) which somewhat agrees with N. E. Brown's statement

(Fl. Trop. Afr. **6**[1]: 471. 1911) to the effect that, "in a few of the terete-stemmed and spiny succulent species [of *Euphorbia*] the involucre-glands are united into one continuous rimlike gland or with only a faint indication of lobing; in these there is nothing but habit to separate them technically from *Synadenium*." So great is the authority of Boissier and Pax, however, that N. E. Brown indorses *Synadenium* without further qualification.

3rd) Is the inflorescence of *Euphorbia* an anatomic constant: that is, are its flowers and their involucres anatomically alike, and constant, in all the species of the genus?

The answer is no. The involucres may have a peculiar shape (*E. pedilanthoides*), colors that exceed the limit of the cyanic and of the xanthic series, hard texture (*E. sclerocyathium*) and a greater or lesser degree of adnation to the axis that supports the female flower as in most *Euphorbiae* sect. *Anthacantha*[2] and in *E. virgata*. The nectarium (the writer prefers this term to the commonly used "gland"), and its appendages vary bewilderingly (*E. leucodendron*, *E. Antso*, *E. fulgens*, *E. clavidigitata*, *E. pauciflora* Duf., *E. pauciflora* var. *pectinata*, *E. cinerascens*, *E. noxia*, *E. Caput-Medusae*, *E. biglandulosa*, *E. corollata*, *E. antiquorum*). The male flowers mostly have staminodia in *E.* sect. *Diacanthium* and are generally without them in *E.* sect. *Tithymalus;* they are fascicled in Indian species of sect. *Diacanthium*, more or less irregularly arranged in curls in other species; free, or partly or wholly surrounded by septa from the involucre (*E. fulgens*, *E. splendens*). The ovary, usually 3-locular, is distinctly 2-locular in *E. Intisy*, and mostly 2-locular, although evidently by abortion in *E. bilocularis* and *E. tetraptera*. The styles are usually discrete, subulate and entire in *E.* sect. *Goniostema*, connate to various heights, lobulate and cleft in *E.* sect. *Tithymalus*. The mature capsule is variously winged or armed (*E. tetraptera*, *E. cybirensis*), indehiscent (*E. akenicarpa*), or projectile (most herbaceous species). The epicarp is fleshy (*E. abyssinica*, *E. pachysantha*), spongy (*E. Lathyris*), or dry (most species). The seed is more or less thickly arillate (*E. Chamaesyce*, *E. Peplis*), carunculate (*E.* sect. *Tithymalus*), ecarunculate (*E.* sect. *Anisophyllum* and sect. *Diacanthium*). These variations are but a few of the many that a careful check of all the known species would reveal.

The answer to the above questions leaves the cyathium of *Euphorbia*, and of the genera segregated from it, in a position which is unmatched by that of any other inflorescence in taxonomy. This peculiar inflorescence belongs to many genera but is commonly used to define precisely only one;

[2] The "sections," here introduced for the sake of brevity, are taken from Boissier in D. C. Prodr. **15**[2]: 7–187. 1862, and from Pax in Engler, Veget. Erd. **9**: 1–168. 1921.

it is not subject to the rules that govern other inflorescences in botanic interpretation; it fails certain genera (cfr. note of N. E. Brown on *Euphorbia* and *Synadenium* (o.c., l.c., quoted above)) but, then, the habit of the plant takes its place; it reunites species that are unrelated in degree of evolution; it is not anatomically constant either in its parts or in the flowers it contains, but the characters derived from its variations are powerless to delimit clearly defined genera.

What, then, is this cyathium? What is its value in taxonomy?

What the cyathium really is we shall soon see. Its value in taxonomy can be judged by the results it yields and by the method it forces upon those who elect it, in whole or in part, as *the* generic character. We see that the cyathium is a myth, a wholly unnatural character, like the drupe or the corolla that in the works of the *artificial* classification defined unrelated groups of plants, *fructu drupaceo donatae* or *corolla papilionacea praeditae*. The cyathium has its place in the works of Tournefort and of Linnaeus: it can not alone serve modern botany, and that is not surprising if one remembers that modern botany claims to be natural and that the cyathium is an inflorescence, not a flower.

So far in principle. In practice the untenable position into which the cyathium-myth forces the Linneists, who fundamentally use it as a flower, and the Anti-Linneists who pull it apart in search of "floral characters" can be shown in Pax's Die Phylogenie der Euphorbiaceen (Bot. Jahrb. **59:** 129–182. 1924.) This work is considered a classic and it makes abundantly clear that the cyathium-myth is inconsistent with scientific interpretation generally, least of all with a natural system of classification.

In 1907 H. Schmidt proposed the monotypic genus *Diplocyathium* based on *E. capitulata* Reich. The species is *prima facie* a member of sect. *Tithymalus* (cfr. Reichenb. Icon. Flor. Germ. Helv. **5:** 1841 fig. 4759a, pl. cxxxvi.) The genus, however, is strictly "orthodox": the species constantly has a double or multiple involucre, and nectaria (glands) to fit the number of involucres.

According to Pax (o.c., 151), the understanding of the phylogeny of *Euphorbieae* requires that the proper value be placed upon *Diplocyathium*. The multiple involucre of the type may be considered a specific character, and it may be asked how the structure came to be. Abnormalities in the cyathium are in the record, but since *E. capitulata* constantly exhibits a multiple involucre *Diplocyathium* must be considered valid. Thus is *Diplocyathium* an archetype. In obedience to these principles Pax draws a phylogenetic tree in which *Diplocyathium* is separated, graphically, at least, from *Euphorbia* by *Anthostema*, *Dichostema*, and *Calycopeplus*, and is shown to be farther remote from *Euphorbia* than *Stenadenium*.

The concepts underlying Pax's understanding of the matter do not come in for discussion here. The nomenclatural validity of *Diplocyathium* might be admitted because the earlier *Diplocyathia* N. E. Brown (*Diplocyathius* K. Schum.) belongs to Asclepiadaceae. It is questionable if not reprehensible, however, that Pax accepts *Diplocyathium* and rejects, e.g., *Epurga*, and neglects the "orthodox" genera required by *E. pedilanthoides* and *E. sclerocyathium*. Furthermore: in phylogeny *E. palustris* might be more interesting than any of the species mentioned: its ovary exhibits peculiar facts (cf. Ber. deutsch. bot. Gesell. **29:** 430–436. 1911.) Once the way is clear, in the name of orthodoxy Rafinesque's "species-genera" must be outdone.

A *natural* classification must not use artificial characters. If *E. capitulata* is an archetype and it can with reason be assimilated sooner to *Euphorbieae* from Africa and Australia, than to *Euphorbia*, its unique position must be supported by an evidence stronger than a double or multiple involucre. But for this, it has been noticed, *E. capitulata* takes rank within sect. *Tithymalus*.

E. capitulata is reported from the high mountains of Dalmatia, Albania, Jugoslavia. This range stood as a zone of refuge during glacial quaternary times, and, as one expects, is rich in species and in forms that exhibit ill defined characters, or are strictly endemic (*E. veneta*, *E. Tommasiniana*, *E. filicina*, *E. dalmatica*, *E. triflora*, *E. Jacquinii*, *E. epithymioides* (*E. fragifera* Jan.) The affinities of the species are with *E. Schottiana* (Cilician Taurus) and it seems, with *E. monocyathium* (Altai, Trans-Altai, Pamir). Its floristic status is precisely the status of *E. herniariaefolia* (Greece to Mesopotamia), *E. caudiculosa*, *E. bounophila*, *E. Aucheri*, *E. Kanaorica* (Asia Minor to India), *E. Valliniana*, *E. ventosica* (Western Alps), *E. chamaebuxus*, *E. pauciflora* (Pyrenees). The axis of range *E. capitulata—E. Schottiana* is very nearly parallel to the axis of the range *E. Broteri—E. pectinata; E. taurinensis—E. sareptana; E. nicaeensis —E. tinctoria; E. glebulosa—E. dracuncoloides* etc. In brief: *E. capitulata* is an alpine relict, a floristic aspect by no means uncommon in the flora of Europe, Northern Africa, Western Asia, which is still largely dominated by the fact of quaternary glaciations. Only an *artificial* character can assimilate *E. capitulata* to anything but to *E.* sect. *Tithymalus*. The species is a recently fixed one, not an archetype.

In the present state of the question the writer admits to prefer the concealed agnosticism of Boissier to the strictly "orthodox" yet palpably false assumption of *Diplocyathium*, and to the attempts at generalization that assume that the Linnean genus must be a "good" genus. This genus is "good" or "bad" *not because one wishes it*, but because the facts, and

an interpretation of the facts in harmony with the basic assumption of natural classification prove it to be true or fictitious. The record conclusively shows that much spade work remains to be done in order that the full implication of the concepts of the classification now in use can be grasped. Not all the facts have been found, and it is certainly difficult to find them. It is unfortunate that no monographic work is later than Boissier's treatment arranged *seventy-five years ago*. Taxonomists working in their own floristic domain may not be expected to compare a species, e.g., of Brazil with the species of Somaliland, Indochina, Australia and the Hawaiian Islands for the sake of deciding whether, fundamentally, Millspaugh is right in postulating *Chamaesyce*. For three quarters of a century the label "*Euphorbia*" has very conveniently gathered in hundreds of species separately presented which fell in with the Boissierian understanding and the Linnean definition because they exhibited a cyathium. Use and necessity, however, are not the criteria by which the truth of a postulate can ultimately be gauged.

Seven American melastomes

H. A. Gleason

Meriania Simsiana Gl. sp. nov. Lignosa ubique glabra; internodia superiora 1 dm. longa superne paullo incrassata tenuiter alata, alis usque 2 mm. latis; folia sessilia verisimiliter amplectentia membranacea ovato-lanceolata, usque ad 28 cm. longa 12 cm. lata, acuta, integra, inferne late rotundata ad basin cordatam, sinu angusto, 7-pli-nervia, jugis 2 externis basalibus in lobos decurvatis, jugo superiore 15 mm. ultra basin folii oriente; venae secundariae supra obscurae subtus rubro-brunneae subplanae, e costis sub angulo fere recto divergentes; venulae tertiariae numerosae reticulatae; panicula terminalis 15 cm. longa multiflora, axi anguste alato; pedicelli circa 2 mm. longi; flores 5-meri; hypanthium obconico-campanulatum 8.5 mm. longum; calycis tubus 2 mm. longus, lobis late rotundatis 0.5 mm. longis; petala immatura; filamenta immatura latissima; anthereae fere 8 mm. longae, connectivo ad antheram adnato crassissimo truncato fere 4 mm. longo; ovarium liberum 10-costatum.

Type, *Rimbach 211*, collected at (or between?) Chimbo and Balsapampa, Ecuador, alt. 2600 m., and deposited in the Britton Herbarium. The species is a member of the section Pachymeriae, and differs from the other species in its sessile pli-nerved leaves with cordate bases.

Graffenrieda trichanthera Gl. sp. nov. Arbuscula 3 m. alta; rami crassiusculi cinerei glabri, cortice sicco ruguloso; petioli crassi glabri, usque 10 mm. longi; laminae coriaceae lanceolatae, maximae usque 135 mm. longae 37 mm. latae, minimae terminales 45 mm. longae 17 mm. latae, omnes acutae integrae basi rotundae glabrae sub-3-pli-nerviae; venae primariae supra impressae subtus prominentes ad marginem approximatae, secundariae sub angulo 70° divergentes, tertiariae obsoletae; capitula florum dense conferta sub-9-flora; flores sessiles 4-meri; hypanthium tubuloso-campanulatum 3.7 mm. longum minutissime puberulum, pilis adpressis fulvis; calyx primum ovoideo-conicus corollam includens usque 1.4 mm. longus, ad anthesin in lobos 2–4 scariosos irregulariter ruptus; petala obovata 3.2 mm. longa 2.3 mm. lata obtusa glabra aequilatera obscure 5-nervia; stamina isomorpha; filamenta glabra erecta 2.9 mm. longa basi dilatata basi contigua et annulum circum torum formantia; antherae subulatae arcuatae 4.6 mm. longae, poro ventro-terminali dehiscentes, thecis infra medium convolutis, connectivo in medio antherae paucisetoso, basi in calcar 0.5 mm. longum minute setosum producto; ovarium liberum ellipsoideum 2.3 mm. longum glabrum 4-loculare; stylus gracilis glaber 8.5 mm. longus, stigmate punctiformi.

Type, *Klug 3298*, collected at Zepelacio, near Moyobamba, Dept. San Martin, Peru, alt. 1100–1200 m., and deposited in the Britton Herbarium. The species of *Graffenrieda* greatly need reclassification. Among those

published, *G. laurina* Triana is possibly the most similar to ours, but differs in its wider leaves, much larger flowers, definitely lobed calyx, and general habit.

Miconia leucantha Gl. sp. nov. Sect. Tamonea: arbor usque 18 m. alta; rami fistulosi juventute 4-angulati leviter sulcati minutissime cinereo-furfuracei demum teretes glabri; petioli graciles 3–5 cm. longi minutissime cinereo-furfuracei; laminae membranaceae virides ovato-ellipticae, usque 15 cm. longae 8 cm. latae, in caudam linearem obtusam 2 cm. longam 2 mm. latam angustatae, basi obtusae vel subrotundae, 5-nerviae, utrinque glabrae; venae primariae supra planae subtus elevatae saepe rubescentes, secondariae fere rectae, sub angulo fere recto divergentes; panicula late pyramidata, 8 cm. longa, axi ramisque 4-angulatis sulcatis minutissime stellato-furfuraceis; pedicelli crassi 1 mm. longi; flores 5-meri; hypanthium campanulatum 3 mm. longum stellato-furfuraceum; calycis tubus 0.4 mm. longus, lobi late depresso-ovati e sinubus angustis 1 mm. longi, extus furfuracei; petala extus cinerea furfuracea, intus glabra rubescentia, oblique ovata, 5.5–6 mm. longa, oblique truncata vel retusa, latere longiore saepe acuta; stamina paulo dimorpha; filamenta 5.3 vel 6 mm. longa, usque ultra medium dense glanduloso-puberula; antherae subulatae paulo curvatae, 4.8 vel 5.7 mm. longae, poro minuto terminali dehiscentes, thecis paulo convolutis, connectivo basi minutissime bilobo, in ser. ext. dorso glandulis 3–4 stipitatis ornato; ovarium fere superum 3-loculare truncato-conicum minutissime puberulum; stylus fere rectus 10 mm. longus, usque ultra medium dense glanduloso-puberulus; stigma capitatum.

Type, *Skutch 2500*, collected in the vicinity of El General, Prov. San José, Costa Rica, alt. 1010 m., and deposited in the Britton Herbarium. *M. leucantha* is clearly closely related to *M. caudata* (Bonpl.) DC., which it resembles in general habit and in most of its structural features. The pubescence of each consists of minute stellate hairs, which in *M. caudata* are twice as large, more densely crowded, and especially developed on the lower side of the leaves, where they form a continuous brown indument; in *M. leucantha* the leaves are strictly glabrous beneath. The petals of *M. leucantha* are nearly twice as large as those of *M. caudata*, and its filaments and styles are densely glandular; in *M. caudata* both filaments and styles are nearly glabrous. The anthers of *M. leucantha* are slightly larger and in one series bear a few stalked glands on the back.

Miconia flaviflora Gl. sp. nov. Sect. Tamonea: arbuscula 8 m. alta; ramuli juniores primum leviter obtuseque 4-angulati ferrugineo-furfuracei, mox subteretes et glabri; petioli 12–22 mm. longi crassiusculi supra canaliculati subtus rotundati fere glabri; laminae subcoriaceae oblongo-ovatae 10–15 cm. longae 3.5–5.5 cm. latae, breviter sed argute caudato-acuminatae, integrae, basi acutae vel subcuneatae, 3-pli-nerviae, jugo minore submarginali neglecto, supra glabrae opacae, subtus brunnescentes minutissime stellato-lepidotae;

venae secundariae rectae 3–4 mm. dissitae, sub angulo ca. 75° divergentes, supra planae subtus conspicue elevatae; venulae utrinque fere obsoletae; inflorescentia paniculata 10–15 cm. longa multiflora, axibus 4-sulcatis tenuiter brunneo-lepidotis; flores 5-meri in cymulis paucifloris terminalibus dense conferti et sessiles; hypanthium campanulatum ad torum 2 mm. longum, supra ovarium leviter angustatum, tenuiter stellato-lepidotum; calyx ca. 1 mm. longus, velut hypanthio pubescens, mox irregulariter ruptus in lobos 5 triangulares ca. 0.5 mm. longos; petala anguste oblongo-obovata obtusa 3.5 mm. longa 1.2 mm. lata, ad anthesin reflexa extus minutissime puberula; filamenta glabra 2.2 mm. longa; antherae fere isomorpha crasse lineares leviter arcuatae, majores 2.8 mm. longae connectivo basi truncato, minores 2.3 mm. longae connectivo basi brevissime 3-lobato; ovarium inferum 5-loculare; stylus glaber; stigma subcapitatum.

Type, *Klug 3697*, collected at Zepelacio, near Moyobamba, Dept. San Martin, Peru, and deposited in the Britton Herbarium. In its leaf-habit, venation, pubescence, elongate petals, and anthers *M. flaviflora* is undoubtedly close to *M. acuminifera* Triana. Early collections of the species, all in bud, were reported by me as the latter species in 1931 (Bull. Torrey Club **58**: 226). Flowering material shows that the petals of *M. flaviflora* are only half as long as those of *M. acuminifera* and that the calyx is much more deeply lobed.

Miconia semisterilis Gl. sp. nov. Sect. Glossocentrum: arbuscula 8 m. alta; rami superiores acute 4-angulares et 2-sulcati dense adpresseque brunneo-lepidoti demum glabrescentes; petioli crassi angulati ca. 1 cm. longi lepidoti; laminae papyraceae anguste ellipticae usque ad 17 cm. longae 6 cm. latae utrinque acuminatae integrae supra glabrae opacae subtus dense cinereo-lepidotae 5-pli-nerviae, jugo exteriore submarginali, jugo interiore ca. 1 cm. ultra basin divergente; venae supra leviter impressae, subtus prominulae; venae secundariae sub angulo 70° adscendentes inter se 3–5 mm. dissitae, tertiariae subrectae vix reticulatae supra obscurae; panicula terminalis 8–10 cm. longa ramosa multiflora lepidota, rhachidibus valde angulatis; flores 5-meri sessiles; hypanthium hemisphaericum 1.1 mm. longum dense lepidotum; calycis tubus 0.3 mm. productum erectum lobis vix evolutis dentiformibus; petala alba obovato-oblonga 1.8 mm. longa 1.6 mm. lata inaequilateraliter truncata glabra; stamina fere isomorpha; filamenta gracilia 1.6 mm. longa; antherae 1.5 mm. longae infra medium steriles ultra medium fertiles obovato-dilatatae 2-loculares poro magno terminali dehiscentes; connectivo infra insertionem filamenti in lobos 2 minutos laterales et lobum 1 (rariter 2) dorsalem anguste oblongum producto; ovarium $\frac{2}{3}$ liberum, ut videtur 3-loculare, summo ovoideo glabro, ovulis ca. 12; stylus crassus 2.6 mm. longus glaber, stigmate truncato 0.5 mm. diam.

Type, *Klug 3224*, collected in forest at Pumayacu, Dept. Loreto, Peru,

and deposited in the Britton Herbarium. The peculiar anthers, sterile for more than half their length and somewhat obovate in the terminal fertile portion, characterize the species and suggest an affinity with *M. Pilgeriana* Ule and *M. stellipilis* Cogn. All three agree further in the appendages of the connective. I have previously offered the opinion that these last two, described originally in the section *Cremanium*, probably belong rather in *Glossocentrum*. Our species differs from these two in its sharply angled stem and lepidote indument. In the last feature it suggests *M. Klugii* Gl., in which the anthers are fertile nearly to the base.

Miconia longisepala Gl. sp. nov. Sect. Amblyarrhena: arbuscula glabra 5 m. alta; rami superiores graciles leviter 4-angulati ad nodos vix incrassati, internodiis 1–2 cm. longis; petioli graciles 10–15 mm. longi; laminae firmulae ellipticae 6–8.5 cm. longae, 2.5–3.5 cm. latae, anguste abrupteque acuminatae in cuspidem linearem 10–15 mm. longam, integrae, basi in petiolum cuneatae, 3-nerviae (jugo obscuro marginali neglecto); venae primariae supra leviter impressae subtus prominulae in acumine approximatae, secundariae utrinque planae subflexuosae sub angulo 60–70° adscendentes, tertiariae supra obsoletae subtus reticulatae; panicula ramosa vix pedunculata 7 cm. longa, ramis oppositis 2–3-floris; pedicelli graciles, ut videtur circa 8 mm. longi sed infra flores nodosi et pedicelli veri tantum 0.5 mm. longi; flores 5-meri; hypanthium subglobosum 3.5 mm. longum rugulosum; calycis tubus vix evolutus, lobi patuli vel reflexi lineari-oblongi 3.2 mm. longi acuti, dentibus exterioribus linearibus teretibus 0.8–1.0 mm. longis sepala subaequantibus et ad sepala arcte adpressis; petala reflexa late oblonga 5.6 mm. longa 3.6 mm. lata inaequilateraliter retusa; stamina fere isomorpha inter se paulo variabilia; filamenta crassa complanata 2.7–3.4 mm. longa dense glandulosa praecipue prope apicem glandulis subsessilibus; antherae semi-ovoideae 2.4–3.0 mm. longae 4-loculares poro minuto ventro-terminali dehiscentes, connectivo simplici; ovarium semi-inferum 5-loculare, parte libera conica glabra 10-sulcata; stylus crassus 8 mm. longus glandulosus, glandulis infra medium minimis brevissime stipitatis, prope apicem majoribus subsessilibus; stigma rotundato-peltatum, 2–3 mm. diam.

Type, *Klug 3233*, collected in forest at Pumayacu, Dept. Loreto, Peru, alt. 600–1200 m., and deposited in the Britton Herbarium. In its general habit and inflorescence and especially in its glandular stamens and style, *M. longisepala* shows its affinity to a group of ten Andean species, of which *M. floribunda*, *M. majalis*, *M. macrantha*, and *M. grandifolia* are probably best known. It is the only species of the group, as far as known to me, with distinctly 3-nerved leaves and it differs from the rest still more notably in the remarkably long sepals which nearly equal the hypanthium.

Miconia expansa Gl. sp. nov. Sect. Amblyarrhena: frutex 3 m. altus; rami superiores exacte 4-angulares glabri, nodis superne sensim dilatatis; petioli

crassi quam laminis 5–8-plo breviores; laminae membranaceae obovato-oblongae breviter abrupteque apiculatae (apiculo 2–5 mm. longo anguste triangulari) integrae sparse glanduloso-ciliatae (pilis 0.5 mm. longis saepe incurvis) basi late cuneatae utrinque glabrae 5-pli-nerviae, jugo obscuro marginali neglecto, venae supra planae obscurae; venae secundariae sub angulo ca. 70° adscendentibus inter se 2–4 mm. dissitae subtus planae, tertiariae supra obsoletae subtus arcte reticulatae; panicula terminalis ampla 16 cm. longa, fere glabra tantum ad nodos sparsissime furfuracea, ramis 7 a nodo superiore, quorum jugo infimo 4 cm. longo paucifloro, terminale elongato multifloro; rami paniculae saepissime 2 in quoque latere a nodis superioribus, superiores oppositi, omnes superne sensim dilatati et valde 4-alati; ramuli supremi breves 1-flori, pedicello tereti brevissimo; hypanthium campanulatum carnosum glabrum 4 mm. longum; calycis tubus non evolutus; sepala ad torum distincta suberecta late ovata glabra 2 mm. longa fere totidem lata, ad apicem obtusam brevissime glanduloso-setosa; petala carnosa alba rotundato-ovata 4.7 mm. longa 4 mm. lata; stamina isomorpha; filamenta crassa erecta complanata 3 mm. longa prope apicem pauciglandulosa; antherae semiovoideae 2.7 mm. longae 4-loculares; connectivum simplex prope basin nonnunquam pauciglandulosum; ovarium inferum 5-loculare, parietibus internis minute foveolatis, summo radiatim costatum et circum stylum depressum; stylus crassissimus 5.6 mm. longus, stigmate capitato 1.8 mm. lato.

Type, *Klug 3201*, collected in forest at Pumayacu, Dept. Loreto Peru, alt. 600–1200 m., and deposited in the Britton Herbarium. This is another member of the same group typified by *M. floribunda* and *M. grandiflora*, and differing from all of them in the conspicuously winged branches of the inflorescence.

New York Botanical Garden

INDEX TO AMERICAN BOTANICAL LITERATURE
1931–1936

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

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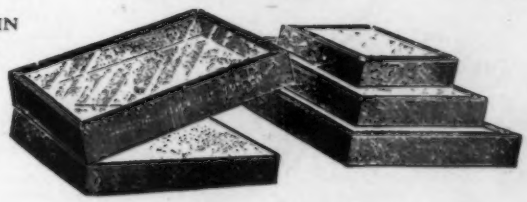

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